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Vivipary and pseudovivipary in the Poaceae, including the first record of pseudovivipary in *Digitaria* (Panicoideae: Paniceae)

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Abstract

This paper reviews and adds information about the phenomena of vivipary and pseudovivipary in the Poaceae, which are reported from 21 genera belonging to subfamilies Pooideae, Panicoideae and Chloridoideae. A previously overlooked description of pseudovivipary in *Digitaria angolensis* is confirmed and constitutes the first record of pseudovivipary in the genus *Digitaria*. This species is illustrated for the first time and the proliferation phenomenon in the spikelets is described and documented.

Keywords: *Digitaria angolensis*; Paniceae; Poaceae; Pseudovivipary; Vivipary

1. Introduction

The term vivipary in a strict sense should be confined to the germination of seeds *in situ* without a resting period (Goebel, 1905; Arber, 1965; Font Quer, 1993). The seeds germinate while still attached to the mother plant and the young seedling grows to a considerable length before falling. Vivipary is especially prevalent among Poaceae, where it has been recorded among a number of crop species. In cereals like rye (*Secale cereale* L.), barley (*Hordeum* L.), oats (*Avena* L.) and triticale (*Triticosecale* Wittm. ex A. Camus), the phenomenon has been termed preharvest sprouting, and the term vivipary restricted to maize (*Zea* L.) on the basis that the husk in maize provides a degree of protection from the moist conditions that promote germination that is not evident in the other cereals (Paulsen and Auld, 2004).

The term vivipary has also been used to cover the development of plantlets from vegetative buds that have entirely replaced flower buds, as in *Agave* and *Phormium* (Allan and Cranwell, 1942). This phenomenon is more appropriately referred to as pseudovivipary to distinguish it from vivipary *sensu stricto*. In grasses, the most familiar situation is the conversion of the whole spikelet or part of the spikelet into a leafy shoot. Plantlets of pseudoviviparous grasses are capable of photosynthesis at any stage of their development (Lee and Harmer, 1980) and, after dehiscing from the parent plant and subsequent dispersal, may root and establish more rapidly in a short growing season than seeds from seminiferous varieties (Harmer and Lee, 1978). Pseudovivipary is an asexual reproductive strategy exhibited by some artic/alpine grasses in which leafy plantlets with conserved, advantageous genomes constitute an advantage for stress tolerators in these nutrient-poor habitats (Pierce et al., 2003). Nevertheless, some grasses growing in temperate habitats occasionally show proliferated spikelets as a response to excessively soil humidity, shading and other adverse conditions during a casual flowering that may occur several months after normal flowering time (Martínez Crovetto, 1944, 1945, 1947).

Proliferated spikelets of this type have been recorded throughout the Poaceae in species of the following genera: *Agrostis* L., *Arrhenatherum* P. Beauv., *Briza* L., *Bromus* L., *Cynosurus* L., *Dactylis* L., *Deschampsia* P. Beauv., *Eleusine* Gaertn., *Eragrostis* Wolf, *Festuca* L., *Ichnanthus* P. Beauv., *Koeleria* Pers., *Lolium* L., *Panicum* L., *Paspalum* L., *Phleum* L., *Poa* L., *Sorghum* Moench and *Trisetum* Pers. Most of these

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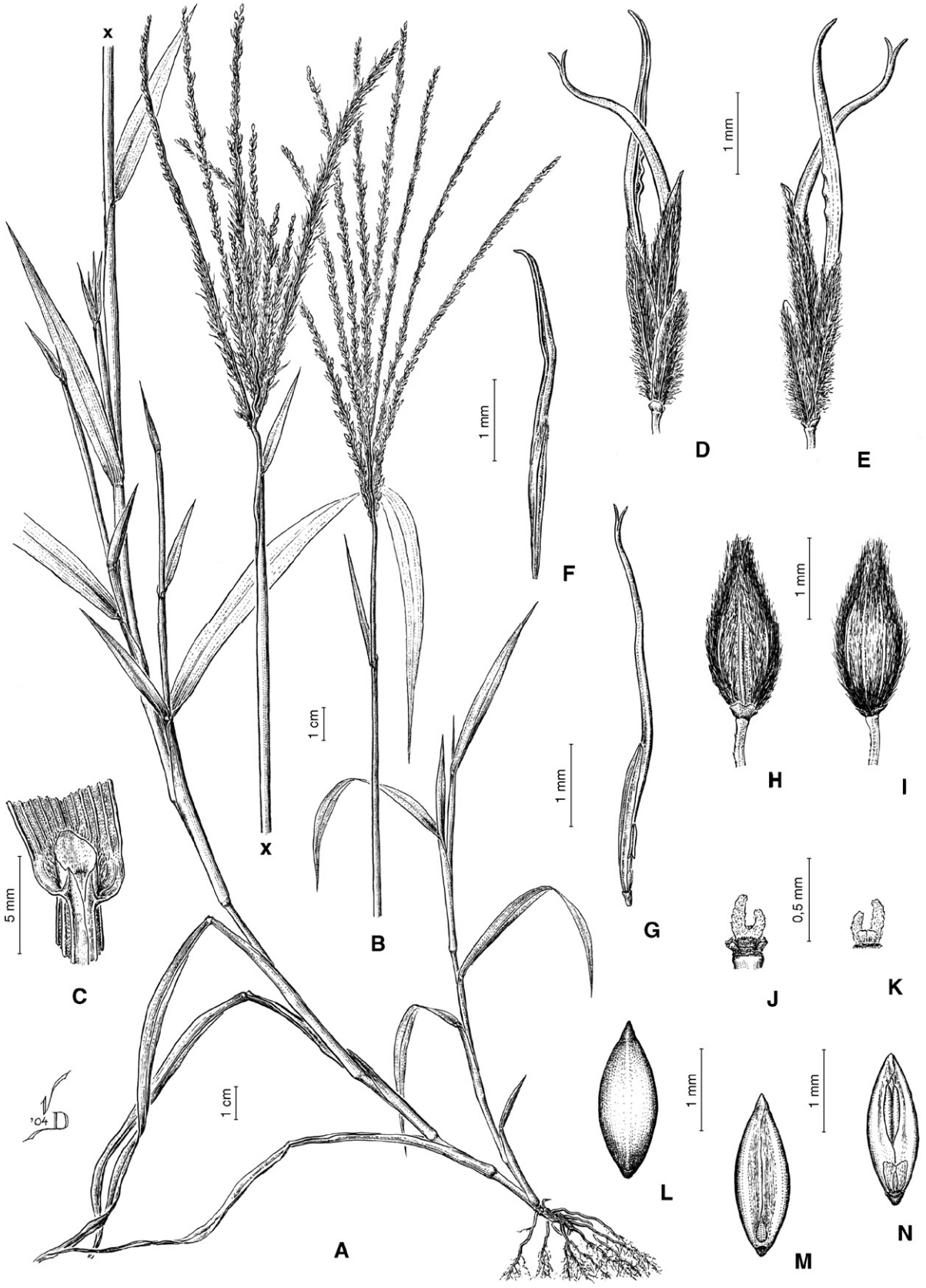

Fig. 1. *Digitaria angolensis*. (A) Habit; (B) panicle (right) and proliferated panicle (left); (C) ligule; (D–E) proliferated spikelets; (F) lower palea and proliferated gynoecium; (G) upper palea, lodicules, stamen and a proliferated gynoecium; (H) "normal" spikelet view from the lower glume and lemma; (I) "normal" spikelet view from the upper glume; (J–K) lower palea; (J) dorsal view; (K) lower palea and lodicules; (L) upper floret view from the lemma; (M) upper floret view from the palea; (N) lodicules, upper palea in ventral view and stamens. *Welwitsch 2790* (BM).

genera belong to subfamily Pooideae. *Ichnanthus*, *Panicum*, *Paspalum* and *Sorghum* are included in subfamily Panicoideae, and *Eleusine* and *Eragrostis* belong to Chloridoideae. Our observation of pseudovivipary in *Digitaria angolensis* (Panicoideae) constitutes the first record of vegetative proliferation of spikelets in a species of *Digitaria*.

The genus *Digitaria* Haller emend. A. S. Vega & Rúgolo has a worldwide distribution in tropical, subtropical and temperate regions of both hemispheres (Watson and Dallwitz, 1992; Vega and Rúgolo de Agrasar, 2001). *D. angolensis* Rendle is an annual species of section *Verrucipilae* (Stapf) Henrard (Henrard, 1950). Originally collected in Angola, *D. angolensis* is widespread through tropical and subtropical Africa, from the Democratic Republic of Congo and Tanzania south to Angola and South Africa (Goetghebeur and Van der Veken, 1989). This species constitutes a weed of arable land and sandy roadsides (Goetghebeur and Van der Veken, 1989), although it is mentioned as infrequent in southern Africa (Gibbs Russell et al., 1990).

The original description of *D. angolensis* (Rendle, 1899) includes the significant observation by Rendle that the spikelets are "often viviparous", although this character has never been mentioned in the genus *Digitaria* and has been overlooked in subsequent floras and monographic treatments of the genus *Digitaria* (Stapf, 1919; Henrard, 1950; Clayton and Renvoize, 1982; Goetghebeur and Van der Veken, 1989; Gibbs Russell et al., 1990). This situation is examined further here.

2. Materials and methods

Observation and descriptions are based primarily on herbarium material at BAA, BM and K (Holmgren et al., 1990).

Digitaria angolensis Rendle, Cat. Afr. Pl. 2 (1): 165. 1899. *Panicum angolense* K. Schum., Bot. Jahrb. 1: 457. 1899. TYPE: ANGOLA. Pungo Andongo: in pratis humidis prope Sansamanda, 2400–3800 ped. elevat., inter 9 et 10° Lat. austr., II-1857, *Welwitsch 2790* (holotype, BM).

2.1. Additional material examined

BURUNDI. Bururi, Rumonge, 3°58′S, 29°26′E, 850 m, 20-III-1981, *M. Reekmans 9850* (BAA). Ruyigi, VI-1950, *R. Germain 7100* (K).

Fig. 2. Type specimen of *Digitaria angolensis* (*Welwitsch 2790*, BM). (A) Herbarium specimen; (B) "normal" spikelets. Bar=0.5 cm. (C) Inflorescence with proliferated spikelets uniformly distributed along the long paraclades. Bar=0.5 cm. (D) Inflorescence with proliferated spikelets restricted to proximal zone of long paracladia. Bar=0.5 cm.

DEMOCRATIC REPUBLIC OF CONGO. Katanga, Parc National de L'Upemba, 1140 m, 21-II-1948, *G. de Witte 3431a* (K).

MALAWI. Dowa, ca. 1 mile S of Bua River, ca. 4000′, 15-II-1968, *Simon et al., 1812* (BM).

UNITED REPUBLIC OF TANZANIA. Tanganyika, Songea district, Songea airfield, 1020 m, 14-III-1956, *E. Milne-Redhead and P. Taylor 9203* (K). Iringa district, Ruaha Nat. Park, 1130 m, 15-II-1973, *A. Bjørnstad AB 2566* (K).

ZAMBIA. Central, Mkushi district, Great North rd. 14 km SW of Mkushi River, 13°36′S, 29°35′E, 1420 m, 3-II-1973, *J. Kornas 3136* (K). Mwembeshi catchment, W. Lusaka I.C.A., ca. 3500′, 17-III-1963, *L. Vesey-Fitzgerald 3963* (BM). Kambowa Agric. Station, Ndola, 3700′, 27-IV-1953, *J. Hinds 118* (K). Mazabuka, Central Research Station, 3800 ft., I-1932, *C. Trapnell 797* (K). Abercorn Dist., 5600 ft., 3-III-1959, *M. McCallum Webster A202* (K).

ZIMBABWE. Norton South Intensive Conservation area, near Selous, Bersheba farm, 20-I-1975, *B. Campbell 233775* (K). Salisbury, Mexico road at 83 km Post S of Salisbury, 1 km E of main hwy, 1370 m, 15-II-1974, *G. Davidse 6684* (K). Centenary, 16-I-1975, *P. Munday 233646* (K). Salisbury, 4800 ft., 9-II-1931, *C. Brain 2486* (BM). West Shiota Reserve, 21-I-1950, *W. Cleghorn 26986* (K).

3. Results

3.1. Spikelet morphology

Most of the specimens studied have normal spikelets (Figs. 1H–N and 2B). Spikelets are 2–2.2 (− 2.5) mm long and 1–1.2 mm wide, and pilose with verrucose hairs shorter than 1.5 mm long that are whitish-silvery with purplish tints, spreading at maturity and exceeding the length of the spikelet by 0.3 mm. The lower glume is 0.2–0.3 mm long, truncate and reduced to a glabrous, hyaline margin more or less embracing the base of the upper glume. The upper glume is subequal to the length of the spikelet, narrower than the upper floret, acute, 3–5-nerved and pilose in the internervial and marginal zones. The lower lemma is as long as the spikelet, membranous, 7-nerved with the three central nerves distant from the marginal contiguous nerves and glabrous on both sides of the mid-nerve but alternately pilose and glabrous in the remaining zones. The lower palea and lodicules are reduced (Fig. 1J–K). The upper floret is 2.0–2.2 mm long, flat-convex with an acute apex, brownish at maturity, longitudinally striate and cartilaginous with membranaceous margins (Fig. 1L–N). The two lodicules are truncate and membranous (Fig. 1N). The anthers are 1.2–1.4 mm long, with purplish tints. The ovary is glabrous and the

Table 1
Viviparous and pseudoviviparous spikelets in the Poaceae

Genera of Poaceae with viviparous spikelets	References
Eleusine Gaertn. (Chloridoideae: Cynodonteae: Eleusininae)	Li, 1950
Hordeum L. (Pooideae: Triticeae: Hordeinae)	Pope, 1941, 1949
Oryza L. (Ehrhartoideae: Oryzeae: Oryzinae)	Claver, 1951
Setaria P. Beauv. (Panicoideae: Paniceae: Setariinae)	Li, 1950
Zea L. (Panicoideae: Andropogoneae; Tripsacinae)	Eyster, 1924, 1931
Genera of Poaceae with pseudoviviparous spikelets (vegetative proliferation of the spikelets)	
Agrostis L. (Pooideae: Poeae: Agrostidinae)	Arber, 1965; Moore and Doggett, 1976
Arrhenatherum P. Beauv. (Pooideae: Poeae: Aveninae)	Arber, 1965
Briza L. (Pooideae: Poeae: Brizinae)	Martínez Crovetto, 1944
Bromus L. (Pooideae: Bromeae)	Nielsen, 1941; Martínez Crovetto, 1945, 1947
Cynosurus L. (Pooideae: Poeae: Cynosurinae)	Penzig, 1922; Martínez Crovetto, 1945; Arber, 1965
Dactylis L. (Pooideae: Poeae: Dactylidinae)	Martínez Crovetto, 1947; Arber, 1965
Deschampsia P. Beauv. (Pooideae: Poeae: Agrostidinae)	Arber, 1965
Digitaria Haller emend A.S. Vega and Rúgolo (Panicoideae: Paniceae: Digitariinae)	Rendle, 1899 cited as "viviparous" spikelets; and this paper
Eleusine Gaertn. (Chloridoideae: Cynodonteae: Eleusininae)	Martínez Crovetto, 1945
Eragrostis Wolf (Chloridoideae: Cynodonteae: subtribe uncertain)	Martínez Crovetto, 1944, 1945
Festuca L. (Pooideae: Poeae: Loliinae)	Nielsen, 1941; Martínez Crovetto, 1945; Arber, 1965; Moore and Doggett, 1976
Ichnanthus P. Beauv. (Panicoideae: Paniceae: Paspalinae)	Martínez Crovetto, 1945
Koeleria Pers. (Pooideae: Poeae: Aveninae)	Martínez Crovetto, 1947
Lolium L. (Pooideae: Poeae: Loliinae)	Martínez Crovetto, 1947; Arber, 1965
Melica L. (Pooideae: Meliceae)	Martínez Crovetto, 1945
Panicum L. (Panicoideae: Paniceae: Panicinae)	Martínez Crovetto, 1944
Paspalum L. (Panicoideae: Paniceae: Paspalinae)	Martínez Crovetto, 1944
Phleum L. (Pooideae: Poeae: Alopecurinae)	Arber, 1965
Poa L. (Pooideae: Poeae: Poinae)	Martínez Crovetto, 1944; Wycherley, 1953; Arber, 1965; Moore and Doggett, 1976; Pierce et al., 2000, 2003
Sorghum Moench (Panicoideae: Andropogoneae; Sorghinae)	Arber, 1965
Trisetum Pers. (Pooideae: Poeae: Aveninae)	Arber, 1965

The generic classification follows Judziewicz et al. (2000), Soreng et al. (2003) and Zuloaga et al. (2003). Subfamily, tribe and subtribe are included in parentheses.

plumose stigma is purplish. The caryopsis is ellipsoid and 1.7 mm long × 1 mm wide; the hilum is 0.3 mm long; the embryo is 1 mm long and shorter than 1/2 of the total length.

3.2. Proliferated spikelets

Proliferated spikelets were only observed in the holotype specimen (Figs. 1D–G and 2). The holotype comprises three plants, each bearing an inflorescence (Fig. 2A). Two of the three subdigitate panicles have proliferated spikelets (Fig. 2C–D). In one of these inflorescences, the proliferated spikelets are uniformly distributed along the long paraclades (Fig. 2C) and, in the other one, proliferated spikelets are generally restricted to the proximal zone of each long paracladium (Fig. 2D). The short paraclades comprise (2)3–4 spikelet-bearing axes of successive branching order; in these short paraclades the degree of proliferation decreases acropetally.

Proliferated spikelets usually have a reduced lower glume and a more developed and foliaceous upper glume, lower lemma and palea, and upper lemma and palea (Fig. 1D–G). The upper glume is 3.5–4.5 mm long, lower lemma 5.0–6.5 mm long, lower palea 1.2–2.5 mm long, hyaline, upper lemma 8–9 mm long, and upper palea 4–5 mm long and 2-nerved. The internodes of the rhachilla between the lower and upper florets are also proliferated and reach up to 2 mm long. The upper floret is modified into foliaceous pieces with the lodicules ±0.5 mm long, three foliaceous staminodia with anthers 1–4 mm long, and a leaf-like structure with a distinct delimitation between sheath and blade with a bifid apex that resembles the gynoecium (Fig. 1G).

3.3. Observation

This species is resistant to Atrazine and Triazine (*Campbell 233775*, K; *Munday 233646*, K).

3.4. Ecology

D. angolensis has been collected from 850 to 2600 m.

4. Discussion

According to Pierce et al. (2003), pseudovivipary has been recorded in 41 species among 13 genera of Poaceae. A review of the literature for this paper increases the number of genera with this phenomenon to 21, belonging to subfamilies Pooideae, Panicoideae and Chloridoideae (Table 1). The recorded occurrence of pseudovivipary in *D. angolensis* has been overlooked in surveys of this phenomenon until now. Proliferated spikelets were detected in two of the three inflorescences of the holotype but not in the additional material examined and thus pseudovivipary seems to be occasional in this species and probably related to some external controlling factor.

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